ON THE DISTRIBUTION OF NEREIS DIVERSICOLOR IN RELATION TO SALINITY IN THE VICINITY OF TVÄRMINNE, FINLAND, AND THE ISEFJORD, DENMARK

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In the literature on the salinity tolerance and osmotic behavior of the widespread estuarine polychaete, *Nereis diversicolor* O. F. Müller, there occur suggestions such as that of Ellis (1937) that physiologically distinct races exist in different regions. Ellis had noted that *N. diversicolor* from Roscoff, France, differed from worms of the same species from Plymouth and Bangor in Britain in rate of weight regulation in response to suddenly lowered salinity, and suggested that the physiological differences observed were of "racial rather than environmental" origin. Unfortunately, Ellis did not report the conditions of salinity under which his experimental animals had existed in nature nor even the salinities at the time and place of collection, so that one cannot decide whether the observed differences in response might reasonably be considered of adaptive significance. Similarly, certain of the findings of Beadle (1937) of differing responses in winter and summer cannot be evaluated because the pattern of salinity variation in the Blythe estuary from which he obtained his worms is not stated.

It is obvious that *N. diversicolor* as a species experiences, and is presumably adapted to withstand, markedly different salinity conditions in different parts of its geographical range. In Britain the species is most characteristic of estuaries, in which it may experience extreme tidal and seasonal variations in salinity, whereas in the tideless Baltic Sea it encounters over much of the year a low but relatively stable salinity. Since the larvae of *N. diversicolor* tend to be benthic (Dales, 1950), populations in British estuaries must be fairly well separated from each other and from those on the continental coasts, and have certainly been isolated for a long time from these of the inner Baltic. Because conditions of extreme salinity variation must present different selective pressures than do conditions of stable low salinity, *N. diversicolor* seems a favorable species in which to investigate the possible existence of physiological races, differing from each other in their tolerance of low salinities. In other words, the character of the distribution of this species is such as to favor the formation of populations genetically distinct in respect to physiological response to low salinity. But while thus suggesting that physiological races in *N. diversicolor* may be a reasonable possibility, we should bear in mind that sound evidence for such races is almost non-existent. In this discussion a physiological race is thought of as a population in which a characteristic and adaptive level of physiological performance exists in response to a given environmental factor, in this instance low salinity. It seems clear that before one can claim to have demonstrated a physiological race of this sort, one must have demonstrated a clear difference in response to the variable factor under comparable conditions in the separate localities, and must also know the pattern of variation of this factor in the different portions of the range of the species. The problem thus divides itself naturally into laboratory studies to measure the response to the controlled variable, in this case low salinity, and field studies to determine the salinity conditions under which *N. diversicolor* lives in representative parts of its geographical range.

The writer has had the opportunity to carry out such studies upon the ecology of *N. diversicolor* and upon its chloride regulation at several selected localities in northwestern Europe, localities which represent three extremes of the salinity conditions within the range of the species.

1. A "marine-dominated" habitat has been studied at Millport, Scotland, and the results reported in a previous paper (Smith, 1955). In brief, the above study (which has been supported by observations in the Salcombe estuary in southern England) shows that *N. diversicolor* when in an essentially "marine" environment finds its optimum in local, relatively brackish, zones.

2. "Stable low salinity" represents perhaps the opposite extreme of the ecological range of *N. diversicolor.* Such conditions are best exemplified in the mesohaline[1] waters of the Baltic Sea, with which the present paper is largely concerned.

[1] Owing to the number of salinity classifications which have been proposed, it is necessary to state that in this paper reference is to the system of Redeke as amended by Välikangas (1933), expressed as salinity in parts per mille (‰). More recently Ekman (1953) has proposed a more complex terminology which embodies essentially the same divisions as the previous one, as seen in the following comparison:

Välikangas (1933)		Ekman (1953)	
Fresh water	< 0.5 ‰	Fresh water	< 0.5 ‰
Oligohaline	0.5–3.0	Oligohaline brackish	0.5–3.0
β (meio-) mesohaline	3.0–8.0	Mesohaline brackish	3.0–10.0
α (pleio-) mesohaline	8.0–16.5	Polyhaline brackish	10.0–17 (20?)
Polyhaline	16.5–30.0	Oligohaline sea water	17 (20?)–30
Ultrahaline (sea water)	> 30.0	Mesohaline sea water	30–34 (?)
		Polyhaline sea water	> 34 (?)

I have elected not to follow the Ekman system because it seems more likely than the older system to lead to confusion as a result of repetition of adjectives, by the use of generally accepted terms in new quantitative meanings, and by the restriction of the term "brackish" to a portion of the range of salinities which it has been taken to cover during long usage. There is much to be said for retaining the general terms oligo-, meso-, and polyhaline to describe waters of low, intermediate, and higher salinities, respectively, and keeping "seawater" for these salinities above 30‰ which characterize the open seas (here some modification of the Välikangas system may be needed). "Brackish" can be omitted as a classificatory term, and the boundaries of the oligo-, meso-, and polyhaline left somewhat flexible, to be adjusted by zoogeographers to fit local conditions (in which it is necessary to state specific salinities anyway). It seems possible that the upper limit of a mesohaline body of water, as judged on faunistic grounds, would be somewhat different in a warm brackish sea than it is in the Baltic, to which both of the above systems rather specifically apply.

It should be noted that the limits of the meio- ("less") and the pleio- ("more") mesohaline of Välikangas have been determined on the basis of Baltic faunas; these divisions thus represent

3. Another type of extreme is represented by "estuarine" habitats such as are common in Britain. Here salinity *variation* is the predominating characteristic, the salinity changing semi-diurnally with tides, often semi-monthly with the lunar cycle, seasonally or erratically with winds and rainfall, and topographically according to relative volumes of estuary bed and fresh-water inflow. Conditions of salinity in the estuarine habitat of *N. diversicolor* are difficult to characterize in any simple way (Bassindale, 1943a, gives one excellent account), and in connection with the present work will be discussed in a later paper.

The results of the comparative physiological work which has been carried out concurrently with observations upon the distribution of *N. diversicolor* in the several areas visited will be assembled in a single paper elsewhere, but it seems advisable to summarize the ecological studies on each type of habitat separately. The attempt to carry out both field and laboratory studies in several widely separated localities within the space of a year has necessarily resulted in a superficial picture. Nevertheless, these studies are probably the first attempt to see *N. diversicolor* with the same eyes over so wide an ecological range, and to support laboratory studies of its salinity tolerance by systematic field observations. It is hoped that our picture of this species may be somewhat clarified, if only by defining gaps in our knowledge. The present paper reports observations made on the south coast of Finland, not far from the eastern limit of *N. diversicolor* in the Baltic Sea, together with subsequent observations in a Danish fjord of comparably stable but not so low salinity. A summary of ecological conditions in each area has been included to complete the picture and as an aid to future visiting workers.

Part I. Observations at Tvärminne, Finland

General description of the area

The Baltic Sea is not only the largest and best-known brackish-water area of the world, but offers in its practically tideless condition a most illuminating contrast to estuarine waters with their tidal fluctuations in level and salinity. For the present study the Tvärminne Zoological Station of Helsinki University has proved most favorably situated. Located on the southeastern side of the peninsula of Hangö at the southern tip of Finland (Fig. 1), it lies near the eastern limit of the range of *N. diversicolor* (Välikangas, 1933), in the west-east gradient of decreasing salinity of the Gulf of Finland. This Gulf is essentially a continuation of the central Baltic, not being cut off (as is the Gulf of Bothnia) by a shallow sill or group of islands. The region about Tvärminne has been extensively studied, so that much information is available to support the studies of the short-term visitor. Thus the bottom fauna of the area has been studied by Segerstråle (1933a, 1933b, 1949, 1955), the larger aquatic vegetation by Luther (1951a, 1951b), the bottom micro-fauna by Purasjoki (1945), the hydrography and plankton by Halme (1944) and Halme and Kaartotie (1946), as well as by others, references to whom may be found in the papers cited. One of the regular water-sampling stations of The Institute of Marine Research, Helsinki, lies in Tvärminne Stor-

a regional adaptation of the more widely applicable but less precise term "mesohaline." Ekman's divisions seem to embody the same ideas, but have gone beyond the concept of a characteristic (or "true") brackish-water fauna to express the idea that the waters inhabited by this characteristic fauna are the "true" brackish waters, a somewhat doubtful logical step.

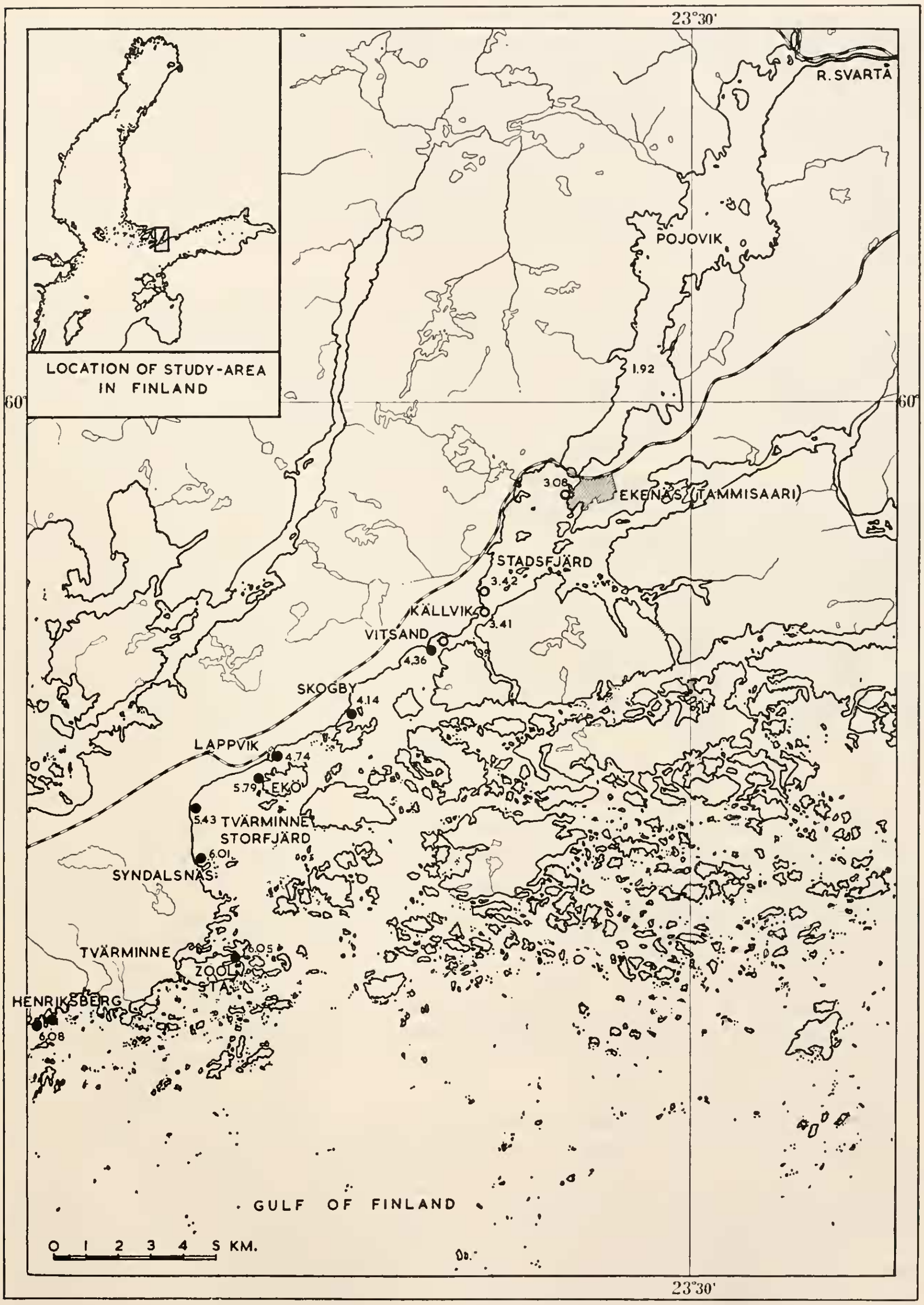

FIGURE 1. Map of the Tvärminne area, Finland, showing localities mentioned in text. Numerals indicate surface salinities observed in July–August, 1954. Black circles, *N. diversicolor* present; open circles *N. diversicolor* not found after careful search on suitable bottom. Detailed data in Table I.

fjärd near the Zoological Station; hence nearly complete series of salinity and temperature records are available for the past 25 years (*e.g.*, Granqvist, 1951). Summer salinities of the open coastal waters near Tvärminne have been about 6°/₀₀ at the surface and 7°/₀₀ at 30 meters (*loc. cit.*). In the past 15 years the region, in common with the rest of the Baltic, has experienced a noticeable rise in salinity of 0.4–0.7°/₀₀ (Granqvist, 1949, 1952). This is not known to have affected the distribution of *N. diversicolor*, but the breeding ranges of certain animals, *e.g.*, *Aurelia*, have been extended eastward (Segerstråle, 1951a), while the amphipod *Calliopius laeviusculus* has extended its range shoreward in the Tvärminne area (Segerstråle, 1953).

Salinity variations in the coastal water mass are quite marked at certain seasons and have been summarized by Segerstråle (1951b). Mainly as a result of the large fresh-water discharge of the River Neva, salinities along the south coast of Finland decrease to the east, and are subjected to further lowering at the time of melting snow. In addition to the main west-east coastwise gradient, there is a gradient of decreasing salinity as one passes northward (inshore) from the outer islands, this gradient being most marked where rivers from the Finnish mainland reach the Gulf. Pronounced salinity stratification may occur, especially when the ice cover prevents mixing by winds. Thus in Tvärminne Storfjärd the salinity of the deeper waters may be almost unaffected by a layer of fresh water from the River Svartå (Fig. 1) flowing beneath the ice (Granqvist, 1938). Its effect upon the bottom fauna of deeper waters must be negligible. Segerstråle (1951b) has shown that spring lowerings of salinity to less than 50% of the annual mean (taken at a depth of 5 meters to avoid the surface layer) occur only about once in 20 years in Tvärminne Storfjärd; the coastal waters are thus of relatively stable salinity. However, in shallow inshore bays the spring dilution may be a much more frequent and serious matter. Thus the Krogarvik, a little bay adjacent to the Zoological Station, whose depth is mostly under three meters and which receives fresh water drainage from a nearby pond and marsh as well as being subjected to the regional lowerings of salinity, may experience salinity reductions to less than 40% of the mean in three years out of four. Segerstråle (1933a) records salinities at the bottom of the Krogarvik as low as 2.02°/₀₀ in 1929 and 0.21°/₀₀ in 1932, although from 1945 to 1950 none lower than 3.77°/₀₀ were recorded (Segerstråle, 1951b). These critical periods of greatly lowered salinity occur in the spring (February–May) and may last as long as a month. The topography of Tvärminne Storfjärd and the Krogarvik are illustrated in Segerstråle's papers (1933a, Abb. 1; 1949, Fig. 4), where more complete descriptions of the region are available.

Tidal changes in water level are virtually absent. A tide of 4 cm. is statistically demonstrable at Hangö (Lisitzin, 1945), but variations caused by local winds and by general water levels in the Baltic are much greater. Thus, during the period of the present study (July 5 to August 9, 1954), the water level at the Zoological Station varied over a range of 40 cm. and averaged 10.3 cm. above mean water level. Luther (1951a) discusses water levels and related matters in some detail, and points out the serious effects which may be caused by low water coincident with the spring discharge of fresh water beneath the ice at shallow inshore localities.

Although to the zoogeographer the distribution of *N. diversicolor* in the west-east salinity gradient of the south coast of Finland is of primary interest, the physiological ecologist with limited time at his disposal finds the local gradient of decreasing salinity from the open Baltic inshore towards the land more convenient for study. The region about Tvärminne receives no fresh water streams of any consequence except for the River Svartå, which discharges a large flow into the northern end of the long fjord-like Pojovik (Fig. 1). This fresh to oligohaline water passes out over deep-lying mesohaline water in the depths of the Pojovik, where the salinity at 30 meters approximates 4‰ (Halme and Kaartotie, 1946), and over a shallow (7 m.) sill at Ekenäs (Tammisaari) into the Stadsfjärd. The latter bay shows a distinct salinity stratification in summer. Halme (1944) describes a labile β-mesohaline wedge of deeper water entering the Stadsfjärd via the narrow but relatively deep (15 m.) strait at Källvik, sometimes extending inwards past the Ekenäs sill and at other times being displaced seaward by the massive outflow of oligohaline water. The Källvik strait thus represents a topographical interruption or discontinuity in the salinity gradient between Ekenäs and Tvärminne Storfjärd, a point to be amplified later.

Segerstråle (1933b) reported that *N. diversicolor* occurred regularly but sparsely on sandy bottoms down to depths of 6–8 meters and occasionally on soft bottoms. The maximum density (44 per $m.^2$) and weight (7.4 gm. per $m.^2$) were obtained on a muddy bottom. Although reported from a number of stations, the species does not appear from this report to have been as abundant at that time as it is at present. Since Segerstråle's stations were restricted to the area about Tvärminne and the southern part of the Storfjärd, the limits of the salinity range of *N. diversicolor* were not known, and a main objective of my field work was to establish the distribution of the species in relation to the local gradient of decreasing salinity inshore from Tvärminne.

Field observations

In the course of collecting worms for physiological work, and on a limited number of other days, water samples were taken at points indicated on Figure 1, and a careful search made for *N. diversicolor*. Quantitative sampling could not be used in the time available; rather, as careful a search as possible was made at each spot on the most suitable bottom, and a rough estimate of abundance based upon the time and effort used in securing specimens. Negative results, where indicated, are based upon at least two visits to the site on separate days under good collecting conditions, employing both visual search and digging in shallow water and dredging in deeper water. All collecting stations were at sites where the bottom appeared to be, on general grounds, suitable for *Nereis*. The most favorable substratum was clearly sandy, ranging in consistency from decidedly coarse on exposed beaches to fine, gray, and firm on protected shores. At deeper levels, worms could be found in mud or gyttja (a soft deposit rich in organic matter), usually with some admixture of sand. Contrary to Segerstråle's experience (1933b) I have obtained the largest specimens in firm sand rather than in mud and at depths of less than one meter. Worms were not taken on clay bottoms, such as were encountered along much of the shoreline of the Stadsfjärd.

Samples were preferably dug with a spade in water up to waist-deep, and washed through a sieve of about one-mm. mesh. On open sandy bottoms it was

TABLE I

Summary of field observations in Tvärminne region

Scale of exposure

E —Exposed
Pr—Protected
SP—Semi-protected

Scale of abundance of Nereis

R—Rare; occasional or single individuals
S—Scattered; consistently found by careful search; 5–10 worms per hour of digging or hand dredging
C—Common; 1 or 2 worms per spadeful or dredge haul
P—Plentiful; several worms per spadeful or dredge haul

Scale of size

L —Large
M —Medium
Sm—Small

Collecting site (see Fig. 1)	Surface salinity ‰	Exposure and substratum	*Nereis diversicolor*		Associated flora (conspicuous elements only)	Associated fauna (conspicuous elements only)
			Abundance	Size		
Henriksberg (outside point)	6.08 (5.95–6.21)	E; coarse sand	S	L	Flocculent or encrusting algae on sand; *Fucus vesiculosus* on rocks	*Macoma baltica* (abundant) *Mya arenaria* *Mysis vulgaris*, etc.
Henriksberg (inside point)		SP; medium sand	F	M and Sm		
The Krogarvik (Zool. Sta.) head and north shore	6.05 (5.99–6.10)	Pr; shallow; fine firm gray sand	S	L	*Fucus vesiculosus* (allochthonous) *Chorda filum* (autochthonous) *Potamogeton perfoliatus* *Ranunculus obtusiflorus* *Myriophyllum spicatum* *Chara tomentosa* *Phragmites communis*	*Cardium edule* (large), *Macoma* (all sizes) *Mytilus edulis* (small), *Mya* (small) *Lymnaea ovata*, *Theodoxus fluviatilis* *Corophium volutator*, *Pontoporeia affinis* *Mesidotea entomon*, *Gammarus* sp. Chironomid larvae, *Dendrocoelum*, etc.
Central parts		Pr; depth 2–3 meters; mud, gyttja, plant remains	C	M and Sm		
Syndalsnäs	6.01	SP; medium sand	P	M	*Phragmites* (otherwise as at Henriksberg	As at Henriksberg
Shore south of Lappvik	5.43	E; coarse sand	C	M	As at Henriksberg but more sparse	*Mya* (large), *Macoma* (small and scarce) *Bathyporeia pilosa*, etc.
Behind point at Lappvik	4.74	SP; medium sand, slightly muddy	C	M and L	Sparse algal mat *Potamogeton*, *Phragmites*, etc.	As at Henriksberg

TABLE I—*Continued*

Collecting site (see Fig. 1)	Surface salinity ‰	Exposure and substratum	*Nereis diversicolor*		Associated flora (conspicuous elements only)	Associated fauna (conspicuous elements only)
			Abundance	Size		
Small bay on Ekö	5.79	Pr; muddy sand below *Fucus*	S	M	Autochthonous *Fucus*, other algae *Phragmites*	*Macoma*, *Mesidotea*, *Lymnaea stagnalis*, etc.
Below Skogby	4.14 (4.09–4.18)	SP; fine muddy gray sand	S	M	Some autochthonous *Fucus* *Phragmites*, etc.	*Macoma* (large and abundant) *Mya* (medium), etc.
Vitsand	4.36 (4.00–4.72) (5 m) 4.81 (10 m) 6.08	SP; fine sand and clay in shallows; mud, coarse sand and debris at 3–5 meters	R; 1 at 4–5 meters	M	*Phragmites* Allochthonous *Fucus*	*Macoma*, and others as in Krogarvik, but restricted to depth below 3 meters
Källvik passage	3.41 (3.10–3.56)	SP; as at Vitsand	Absent		*Phragmites* Allochthonous *Fucus*	In channel, below 5 meters: *Mytilus* (large and abundant), *Mya* and *Cardium* (medium) *Membranipora crustulenta* and *Balanus improvisus* (large and abundant, on *Fucus* and *Mytilus*) Rest of "marine" fauna as in Krogarvik
Southern end of Stadsfjärd	3.42 (2.97–3.87) (5 m) 5.72	SP; as at Vitsand	Absent		*Phragmites*, *Potamogeton*, and other freshwater plants in shallows Allochthonous *Fucus* below 3 meters	In shallows: *Bithynia tentaculata*, *Theodoxus* *Asellus aquaticus*, chironomid larvae, etc. Below 3 meters: *Balanus* and *Membranipora* (common) *Cardium* (small, 1.2 cm.; free in coarse sand) *Macoma* (all sizes, abundant) *Pontoporeia affinis* (abundant), *Mesidotea* (large and breeding) (*Mya* and *Mytilus* absent)
Ekenäs (Tammisaari)	3.08 (2.66–3.49)	SP; fine gray sand, slightly muddy	Absent (no dredging at this station)		*Enteromorpha* Filamentous green algae	*Cordylophora lacustris* (on pilings); *Macoma* at deeper levels (*Mesidotea* beyond this point at deeper levels as breeding resident of Pojovik)

often possible to locate worms by observing the burrow openings; digging at such spots commonly yielded worms where random digging and sifting had failed to reveal a single individual in an hour's time. Hence calm weather permitting a clear view of the bottom was considered a requisite of good collecting conditions on sandy shores fairly free of macroscopic algae, but was of less value in protected bays where algal growth often covered the bottom. Dredging was carried out from a skiff or motorboat, employing a light triangular ring-dredge whose line was weighted with chain to encourage the dredge to bite into the substratum. This dredge would secure a good sample of soft mud and/or coarse sand but proved useless on the type of fine, hard, sandy bottom (as at the head of the Krogarvik) where spading showed the presence of scattered to common very large worms, rather deeply buried.

Salinity determinations have been made as in the previous study (Smith, 1955) by determining chloride in grams per liter on duplicate one-ml. samples. Because all previous reports on the Tvärminne area have used salinity rather than chlorinity, my results in the present work have been expressed as approximate salinity in parts per mille, calculated by multiplying my chloride (essentially chlorosity) values by 1.81. The results are thus not exactly what would have been obtained by routine hydrographic methods, but are close enough for an ecological account.

The field observations are summarized in Table I and the distribution of *N. diversicolor* and of mean surface salinities (deep salinities in table) shown in Figure 1. It may be seen that in all suitable localities from Henriksberg on the outer shore to the vicinity of Lappvik, worms are fairly common in shallow water, but disappear from the shore somewhere above Skogby. At Vitsand *N. diversicolor* could not be found in shallow water despite the presence of apparently suitable bottom, but a single individual was taken by repeated dredging at a depth of 4–5 meters. The species thus reaches its limit outside the constricted Källvik strait, at a point which, incidentally, is also the limit of autochthonous (attached) *Fucus vesiculosus* (Luther, 1951a). No other reduction in the marine fauna has been noted in the deeper water at this point, and it is significant that at a depth of 10 meters the salinity is still as high as at the surface on the outer shore. In the narrow Källvik strait a vigorous marine fauna, except for *Nereis*, also exists. Within the Stadsfjärd we see a drastic reduction of this fauna, with the dropping out of *Mya* and *Mytilus* and the reduction of *Cardium*, as well as the appearance of a number of fresh water forms.

Discussion

A study of Table I reveals several facts, some of which when viewed in the light of other findings are not a little puzzling:

1. In typical tidal estuaries, marine animals generally tend to occupy an upper intertidal level as they extend upstream into less saline waters. While this may be attributable to differences in the position of suitable substratum (as pointed out by Spooner and Moore, 1940, for mud-dwellers in the River Tamar), it has the advantage that the higher salinities of the flood tide are received and the lower salinities of the ebb avoided. But here in the tideless Baltic, the distribution of the worms (which are of course always "subtidal") follows the zone of favorable salinity to a lower level as fresher waters are approached. The salinities actually

encountered by these worms in summer are thus not so low as the surface salinities over the range might imply.

2. It would appear that *N. diversicolor* in the Tvärminne area does not normally have to endure summer salinities below about 4°/₀₀. When we consider that worms of this species living in estuaries have a range extending from salinities of 22°/₀₀ or more down to salinities below 1°/₀₀ (Percival, 1929), and when we further consider the fact observed in the experimental part of this study that worms from any part of the Tvärminne area can at summer temperatures tolerate soft fresh water (chloride about 0.02°/₀₀), it is surprising indeed that *N. diversicolor* is limited in the field at a salinity as high as 4°/₀₀. The obvious conclusion is that the species is not being limited by the salinities prevailing in summer near Tvärminne, but if salinity is a limiting factor at all, it must be operating at some other time of year, most probably during the spring reduction of salinity associated with melting snow. Two possible ways in which the species might be affected are (1) by inability of the adults to perform the necessary osmotic regulation when temperatures are near 0° C. or (2) by a failure in some aspect of reproduction and/or dispersal. The first alternative would imply that *N. diversicolor* could not survive the winter or spring even if it had become established in the Stadsfjärd in the previous summer. We have no specific information on which to base further discussion of this possibility. The second alternative implies that *N. diversicolor,* even if capable of surviving in the Stadsfjärd as an individual, would fail to reproduce itself there, and that larvae produced elsewhere are unable to enter to replenish the population. The available information on the breeding habits of *N. diversicolor* (summarized by Dales, 1950) indicates that in most localities it is a winter or early spring spawner. Although the breeding season at Tvärminne is not yet known, it would appear to have been completed prior to July in 1954. In examining and taking coelomic fluid samples from over 100 worms in the laboratory during the present work, besides handling a much greater number in the field, not a single male has been identified. Female worms, greenish and with obviously over-ripe eggs, were found on several occasions, and worms with small undeveloped oöcytes were numerous, probably representing the next year's breeding stock. Small worms (under 15 mm. in length) were common in collections, and many more undoubtedly escaped through the sieves used. The smallest nereid seen (collected by Dr. T. G. Karling at Henriksberg on August 4) measured 2 mm. in length and had 15 setigerous somites. According to the rates of growth reported by Dales (1950) at unspecified temperatures, this worm was probably 6–8 weeks old. Spawning must then have been essentially completed before the summer months, but whether it fell in or after the spring period of low salinity could only have been determined by field studies at that time.

3. Although in British estuaries *N. diversicolor* penetrates further into waters of low salinity than any other "marine" types except for certain crustaceans which do not enter the present discussion (Percival, 1929; "Plymouth Marine Fauna," 1931; Spooner and Moore, 1940; Bassindale, 1943b), this species in the Tvärminne area is one of the first elements of the characteristic brackish-water faunal assemblage to drop out. To be sure, certain marine types such as the amphipods *Pontoporeia femorata*, *Calliopius laeviusculus*, and *Gammarus locusta*, as well as the isopod *Idothea baltica*, the priapulid *Halicryptus*, the polychaete *Harmothoë sarsi*, and others, seem to be restricted to the highest salinities found about Tvär-

minne. These have been poorly or not at all represented in my collections, and will not be included in the following discussion. Leaving them aside, we see from Table I that *N. diversicolor* does not penetrate as far into lower salinities as do the rest of the animals commonly associated with it. To an observer whose experience has been gained outside the Baltic this fact seems paradoxical, but it would appear that the situation in the shoreward gradient of decreasing salinity from Tvärminne to Ekenäs reflects a condition characteristic of the Baltic as a whole and not unusual in terms of this brackish sea. Thus the ranges shown by Välikangas (1933) indicate that in the gradients of decreasing salinity of both the Gulf of Finland and Gulf of Bothnia, *N. diversicolor* stops short of such forms as *Mytilus, Macoma, Membranipora, Corophium volutator,* etc. Other information indicates that *Mya* extends further into the Gulf of Bothnia than does *Nereis* (Segerstråle in litt.), and *Cardium* further east in the Gulf of Finland (Segerstråle, 1933b). One is thus encouraged to hope that an analysis of the factors limiting *N. diversicolor* in the local salinity gradient shoreward from Tvärminne may shed light upon the more general problem of its distribution in the Baltic Sea. And the closer we can come to understanding why the relative distribution of *Nereis* and its associates in the Baltic is so different from that seen in typical estuaries, the closer are we to understanding the effects of these different environments upon the animals which are able to inhabit them, and the nature of physiological adaptation to such environments.

4. With reference to Table I, the following facts and comments are offered: It may be significant that of the associates of *N. diversicolor* which do penetrate the Stadsfjärd, at least two, *Mesidotea entomon* and *Pontoporeia affinis,* are glacial relicts which are also found in fresh water lakes (Segerstråle, 1955). *Membranipora crustulenta* likewise extends into very low salinities in the heads of the Gulfs of Finland and Bothnia (Välikangas, 1933) and so would not be encountering severe conditions in the Stadsfjärd. Of the properly marine species, *Macoma baltica* is a summer breeder (Segerstråle, 1951b) and would be reproducing when salinity in the Stadsfjärd is maximal. A further point to notice is that *Cardium, Balanus improvisus,* and *Membranipora,* even if unable to reproduce within the Stadsfjärd (a point which has not been confirmed or denied), might have entered it as planktonic larvae at a time of saltwater ingression following the spring outflow; Levander (1915) has recorded larvae of the latter two forms within the Stadsfjärd in summer (at his station VIII). It is also possible that these three species could have been carried in as post-larval stages on drifting *Fucus. Membranipora* in the Stadsfjärd is generally on this plant; *Balanus* is commonly so found. One large individual of *B. improvisus* has been found on a clean pebble weighing 27 grams, suggesting settlement *in situ,* but the possibility that the stone was carried in by *Fucus* at some previous time cannot be entirely ruled out. Likewise, very small *Cardium* are abundant, byssally attached to *Fucus* outside the Stadsfjärd, and could readily drop off after drifting in. But in the case of *N. diversicolor,* the possible planktonic stage is at most a brief one (Dales, 1950), and attachment to allochthonous *Fucus* does not seem a probable means of transport. Although Thorson (1946) reports larvae presumed to be of *N. diversicolor* in the plankton of the Danish Øresund from late March to July–August (with maximum abundance in April and May), there are no records of nereid larvae in

the plankton about Tvärminne. In response to a question on this point addressed to Drs. Purasjoki and Segerstråle, the latter has replied (in litt.) "We are of the opinion that there is rather convincing evidence of the worm not having a planktonic stage in our waters. No such larva has been found in the numberless plankton samples taken since decades, including the cold season." We may further note that a nereid larva entirely lacks a protective shell, and may for this reason be less resistant than larvae of *Balanus* or bivalve molluscs. If conditions in and above the Källvik strait are such as to prevent the reproduction of *N. diversicolor* or the survival of its early larvae, and if the species with its brief and benthic larval life lacks the means of colonizing this region beyond its actual breeding range, then we may consider that the distribution of the species is limited not by one, but by the interaction of several factors. More specifically, the factors which limit the spread of *N. diversicolor* (while permitting the advance of its marine associates) are not restricted to the physiological tolerances of the worm and its larvae, but must include physical factors of hydrographic conditions which may not be favorable to dispersal at the time larvae are produced. The data of Halme and Kaartotie (1946) suggest that the narrow Källvik passage is subjected to greater spring disturbances of salinity at its deeper levels than is any other part of the area studied. If we consider the 5-meter depth as a level likely to be critical for *N. diversicolor* (which has not been reported deeper than 6–8 meters), the records of Halme and Kaartotie show that in 1936–37 the Tvärminne Storfjärd had an annual salinity variation of 1.25‰ (6.45–5.20), the Pojovik varied by 1.35‰ (2.30–0.95), while in the Källvik passage the variation recorded was 2.30‰ (5.25–2.95). This indicates a deep penetration of oligohaline water during the spring discharge, and suggests that the constricted Källvik strait represents a rather abrupt discontinuity in the local inshore salinity gradient. It is thus a hydrographic barrier which may affect the distribution of *N. diversicolor* more adversely than it does that of the associated marine species. If, as seems likely, *N. diversicolor* produces its larvae during the spring lowering of salinity, when there is still a large net outflow past Källvik, there is a good chance that even if the weakly-swimming larvae were injected into the plankton by turbulence, they would either be killed by low salinity or swept seaward. Other marine species with a later breeding season or a longer planktonic existence might be able to pass into the Stadsfjärd when the hydrographic barrier is minimal during the summer. It would be interesting to know if a more gradual salinity gradient leading into some other Baltic river system might not permit *N. diversicolor* to extend its range into salinities as low as it seems to tolerate in estuaries elsewhere. If such a river can be found, it might provide a test of the ideas just expressed.

Conditions in the Krogarvik, the shallow bay close by the Zoological Station, might also prove very illuminating in respect to the possibility that *N. diversicolor* is either limited by inability to regulate osmotically during periods of minimal salinity combined with low temperature in spring, or that its reproduction or larval survival are hindered. Unfortunately, the determinations of salinity at the bottom of the Krogarvik obtained by Segerstråle in the years 1929–32 and 1945–50 have not been continued until 1954. *N. diversicolor* was common in this bay in the summer of 1954, and the largest individuals, which had certainly over-wintered, were found near the head of the bay in water so shallow that they must have been close beneath the ice (unless they had migrated from deeper levels, an undemonstrated possibility). It is perhaps significant that the winter of 1953–54 was unusually free of snow, and it may be that the Krogarvik experienced little reduction of salinity at the spring thaw. I am informed by Professor Palmgren that the taking of salinity samples at the bottom of the Krogarvik will be resumed, and if the winter results can be correlated with the abundance of *N. diversicolor* in each following summer, it may be possible to determine from this natural experiment what salinities can be tolerated by these worms at winter temperatures. Studies of osmoregulatory ability under refrigeration in summer might be helpful, but probably not conclusive because of the ability of some animals to adjust their metabolism to seasonal changes in temperature; studies made in winter would be more informative.

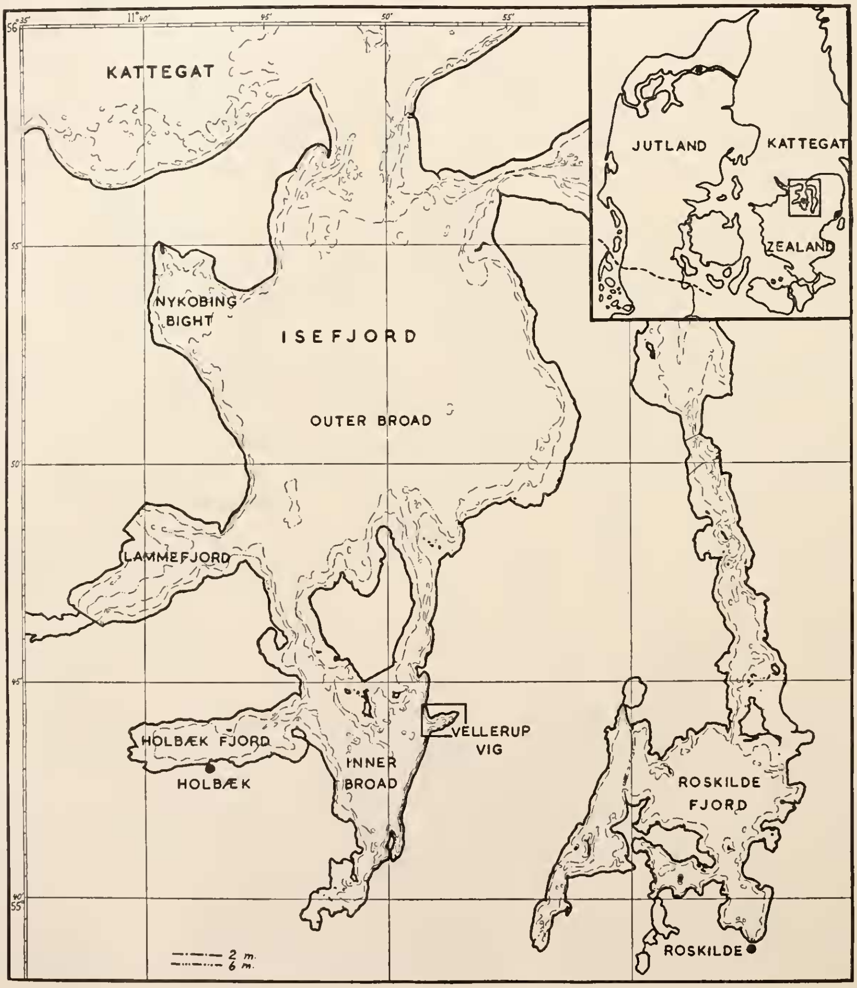

FIGURE 2. Map of the Isefjord, Denmark.

Part II. Observations in the Isefjord, Denmark

General description of the area

In a geographical sense the Isefjord (Fig. 2), in the northern part of the island of Zealand to the west of Copenhagen, is intermediate between British waters and the Baltic, while its mean surface salinity of $20^{\circ}/_{00}$ is midway between salinities at Tvärminne and Plymouth. The hydrography of the Isefjord has been summarized by Nielsen (1951). His account shows that this body of water is characterized by a stability of salinity greater than that of the south Finnish coast. The Isefjord has an area of 280 square kilometers and is so shallow (mostly less

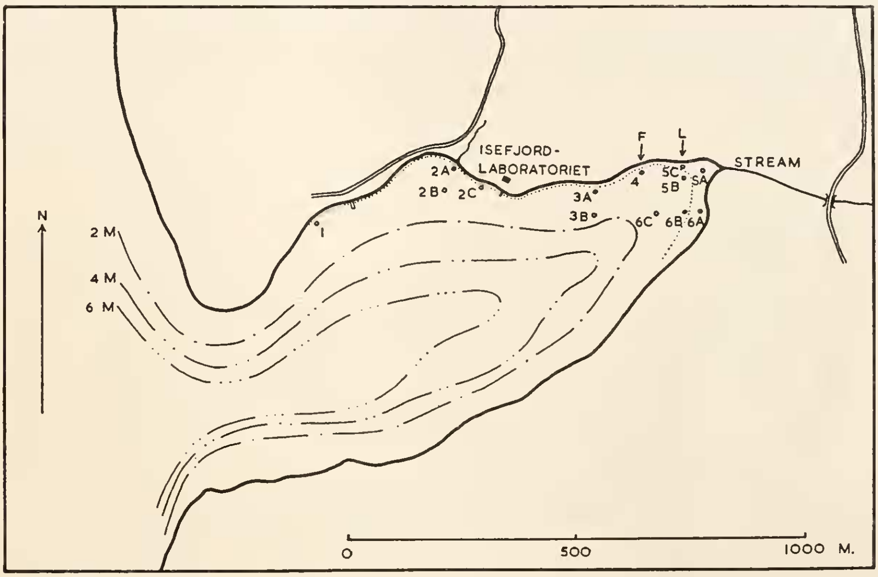

Figure 3. Vellerup Vig, showing sampling stations. Details in Table II. Arrows marked F and L show limits of *Fucus* and *Littorina* on the shore.

than 10 meters) that despite the presence of a sill at its mouth, salinity stratification rarely occurs. According to Nielsen's observations, mean surface salinity in the Inner Broad (southern part of the fjord) is $20.18^{\circ}/_{00}$, with extremes noted of 17.79 and $22.23^{\circ}/_{00}$, while at depths of 4–6 meters the corresponding values are $20.54^{\circ}/_{00}$ (19.03–23.88). The Isefjord is thus polyhaline in the sense of Välikangas (1933). In comparison with conditions near Tvärminne it is notable that the lowest salinity of $17.79^{\circ}/_{00}$ was obtained in March, immediately beneath the ice, and that the difference in salinity between surface and 5 meters at that time was only $4.74^{\circ}/_{00}$. The Isefjord freezes easily and may have an ice cover for three months in cold winters, although there is evidently not such a marked seasonal lowering of salinity beneath the ice as is experienced in Finnish waters. The reason for this is doubtless the slight fresh water drainage into the Isefjord, which has a very small watershed (800 sq. km.) and receives only small streams. So low is the fresh water input that the Inner Broad, the head of the fjord, actually has a mean salinity $0.5^{\circ}/_{00}$ *higher* than the Outer Broad which lies nearer the

TABLE II

Field observations, Vellerup Vig: salinities at low and high water at sampling stations (see Fig. 3) densities of Nereis diversicolor and N. southerni (approx. number per ⅛ sq. meter), and principal associated biota

Key to symbols

F—*Fucus vesiculosus* (autochthonus)
L—*Littorina littorea* (on upper midtidal rocks)
Mt—*Mytilus edulis*
M —*Mya arenaria*
C —*Cardium edule*

Station (see Fig. 3)	Character of station	Salinities ‰		Worm density		Associates
		L. W.	H. W.	*N. div.*	*N. south.*	
1	At L. W. M.; muddy sand	18.40	—	6	1	F L Mt — —
2A	Subtidal, by stream mouth; sand and clay	1.63	17.58	83	4	F L Mt — —
2B	50 meters out; muddy sand, near rocks	15.41	18.40	2	33	F L Mt C —
2C	Subtidal, away from stream; sand and clay	—	—	3	22	F L Mt — —
3A	Subtidal; muddy sand	10.96	13.67	3	41	F L Mt — —
3B	50 meters out; fine sand	12.33	17.21	0	19	— — — M C
4	Subtidal, at limit of *Fucus;* sand	7.73	9.59	75	2	F L Mt — —
5A	Intertidal, under flowing fresh water at low tide; gravelly	0.03	0.62	6	0	— — — — —
5B	Subtidal, at foot of fresh water outflow; gravelly	0.29	0.83	39	0	— — — — —
5C	Intertidal; muddy sand, at limit of *Littorina* on rocks	1.25	4.13	76	0	— L — — —
6A	Intertidal; muddy sand at head of bay	2.32	9.37	134	0	— — — — —
6B	Subtidal; muddy sand	1.88	—	47	1	— — — M —
6C	100 meters from H. W. M.; fine sand	4.05	9.52	5	16	— — — M C

Kattegat. Tides are small, about 20 cm. in mean range, but massive ingression or expulsion of water during gales commonly causes deviations in water level of ± one meter. The Isefjord is thus an area of moderately reduced but exceptionally stable salinity, and it is of interest to learn where *N. diversicolor* finds its optimum within it.

Field observations

The present study has been restricted to the head and northern shore of Vellerup Vig, a small bay on the eastern shore of the Inner Broad (Fig. 3). The intertidal shore is mostly narrow, rather steeply sloped, varying from muddy sand to coarse gravel, covered with stones in more exposed places, and interrupted by extensive patches of reeds (*Phragmites*). A soft flat muddy shore about 25 meters wide is exposed by low tides at the head of the bay. Below low-water mark the bottom is nearly flat, of fine muddy sand with some clay and scattered large boulders which support *Fucus vesiculosus*, *Mytilus edulis*, and *Littorina littorea*, except in the less saline head of the bay. *N. diversicolor* occurs quite generally along the midtidal shore beneath stones resting on muddy sand, but is not abundant sub-tidally except in certain areas which are clearly those freshened by inflowing streams. A good-sized stream enters the bay at its head and a small one just to the west of the Isefjord Laboratory.

In making collections, most worms had to be dug under water, hence direct sampling of quadrats was not feasible, and the method was adopted of filling a cubical box 25 cm. in each dimension by several spadefuls of substratum taken

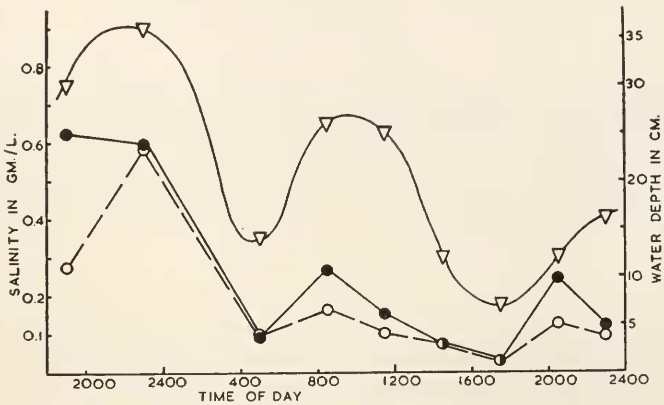

FIGURE 4. Variation in water level and salinity over fringe of population of *N. diversicolor* at station 5A (see Fig. 3) at stream mouth, Vellerup Vig, August 28–29, 1954. Triangles, depth of water in cm.; black circles, salinity at bottom; open circles, salinity at surface.

within an area a few feet across at each station. On the assumption that the digging was effective to about half the depth of the box, the full box would represent an area sampled of ⅛ square meter. The material obtained was sifted through a pair of sieves of ¼- and ⅛-inch mesh. Most of the smallest worms were lost, but the counts obtained are comparable among themselves. Figure 3 shows the positions of collecting stations, and the results of the field observations are summarized in Table II. It is evident that *N. diversicolor* is highly concentrated in the head of the bay and near the mouth of the small stream near the laboratory.

A second nereid, which has been shown to be less tolerant of reduced salinity (Jørgensen and Dales, in press), is also abundant in Vellerup Vig and is being described as a new species, *Nereis southerni*, by Abdel-Moez and Humphries (in press). The populations of *N. southerni* and *N. diversicolor* overlap only very slightly. I am informed by Dr. Erik Rasmussen that *N. southerni* has been increasing in abundance in Vellerup Vig during the past few years, and that it seems to have replaced *N. diversicolor* in areas where the latter used to be of regular occurrence. This fact forces one to exercise caution in seeking to establish the salinity optimum of *N. diversicolor*. The apparent optimum shown in the present studies can only be a restriction of the species to that part of its potential range where it escapes critical interspecific competition. The same problem has been encountered in the case of *N. diversicolor* at Millport, Scotland (Smith, 1955). It is, nevertheless, clear that *N. diversicolor* at Vellerup exhibits a marked tolerance for water of very low salinity, even extending its distribution into areas exposed to outflowing fresh-water at low tide.

At the mouth of the stream at the head of the bay *N. diversicolor* was found in reduced numbers, but still commonly, living intertidally beneath flowing fresh-water for part of each tidal cycle. In order to gain a rough picture of the salinities endured by this vigorous fringe of the population at the extreme of its habitat, water-levels and salinities were measured at intervals over a 27-hour period, and the results are shown in Figure 4. Although no great regularity is revealed, it is evident that these worms can live beneath salinities of less than 1‰ (0.65–0.03‰) for at least a day at a time. It should be noted that the summer of 1954 prior to these observations had been the rainiest experienced in many decades, so that salinities at this spot had probably been even lower than those recorded. On the other hand, it is likely that an occasional high stand of water caused by wind may have provided a temporary respite in the form of a saline wedge forced in beneath the outflowing fresh-water at this point. Figure 4 indicates some salinity stratification near the stream mouth.

Discussion

N. diversicolor collected from the head of Vellerup Vig has been used by the writer in studies of chloride regulation and also by Jørgensen and Dales (in press). Worms from this spot are quite capable of living in fresh water in the laboratory, and apparently some of them endure it for a greater or less time in nature. In my studies of the level of chloride regulation after adaptation to low salinities, I have found no difference between *N. diversicolor* from Finland and from Denmark. This finding of similar regulatory ability is in marked contrast to the distribution of the species in the respective localities. In the Finnish area of prevailing low salinity we find *N. diversicolor* restricted to the more saline part of the potentially available range, even less able to invade oligohaline waters than *Mytilus, Cardium, Mya, Balanus improvisus,* and others. But in the Isefjord, where prevailing salinities are three times higher, *N. diversicolor* is strongly concentrated in the least saline portions of the available range, into which it advances further than any of its marine associates, thus behaving quite like its relatives in British estuaries and unlike those of the inner Baltic Sea.

The factors which determine optimal conditions for a species are complex, and the distribution of *N. diversicolor* in relation to salinity has not, by this study, been reduced to any simpler terms. We have seen that the relative position of the species in the regional salinity gradient is quite different in the Baltic Sea than it is elsewhere, but it is quite possible that the differences in distribution are caused by special hydrographic conditions (in particular, the spring reduction of salinity characteristic of the inner Baltic) rather than by any fundamental or "racial" differences between the worms themselves. The gradient between the polyhaline waters of the Isefjord and the oligohaline conditions near stream mouths is interrupted by no such zone of hydrographic instabliity as the Källvik Strait imposes between the mesohaline and oligohaline waters of the Tvärminne region. It is possibly quite significant that the most unfavorable hydrographic conditions both in the Tvärminne area and in the Baltic as a whole occur at or near the probable time of reproduction of *N. diversicolor*. We have also noted that although the Isefjord as a whole has a mean salinity of about $20^{\circ}/_{00}$, which lies within the optimum salinity range of *N. diversicolor* as seen at Millport (11–$22^{\circ}/_{00}$), the Vellerup population finds its apparent optimum at a much lower absolute salinity. But in both instances the apparent salinity optima may be in part the result of interspecific competition. The studies at Tvärminne and Vellerup, despite their limited scope, emphasize the fact that an ecological optimum must be related to the total life history and physiological capabilities of the species concerned.

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Summary

1. A comparative field study of the distribution of *Nereis diversicolor* near Tvärminne, south Finland and in the Isefjord, Denmark shows that although the species penetrates into nearly fresh water in the Isefjord, its distribution near Tvärminne is limited at summer salinities of over $4^{\circ}/_{00}$.

2. The apparent salinity optimum of *N. diversicolor* on the border of the polyhaline Isefjord is lower than on the "marine-dominated" beach at Millport, Scotland, but in both instances there may be a restriction of the potential range because of interspecific competition.

3. The paradoxical situation is seen near Tvärminne of *N. diversicolor* being among the first of the characteristic brackish-water fauna to drop out as salinity

lessens, whereas in the Isefjord as well as in British estuarine situations it penetrates further toward fresh water than the rest of its associates.

4. It is suggested, on the basis of hydrographic conditions in the Tvärminne area, that salinities prevailing in summer cannot be the limiting factor for *N. diversicolor* in the Baltic Sea, but that critically low salinities occurring in spring while temperatures are still very low may adversely affect the osmoregulation and/or reproduction of the species. Furthermore, there may be a hydrographic (as well as a purely physiological) barrier to the spread of the species into oligohaline waters, in which connection the time of breeding and the lack of a long planktonic stage in the life history may be important.

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